Comput. Math. Applic. Vol. 15, No. 6–8, pp. 555–564, 1988
Printed in Great Britain.
0097-4943/88 \$3.00 + 0.00

HOPF BIFURCATION AND THE STABILITY OF NON-LINEAR AGE-DEPENDENT POPULATION MODELS

J. H. Swart
Department of Mathematics and Applied Mathematics, University of Natal, King George V Avenue, Durban 4001, R.S. Africa

Abstract—The possibility of Hopf bifurcation into stable orbits is considered for the Gurtin–MacCamy model of age-dependent population dynamics, in which the mortality function depends only on the population while fertility is a fairly general function of age as well as population. In addition an algorithm is produced which provides a necessary condition for Hopf bifurcation to occur for arbitrary systems of ordinary differential equations.

INTRODUCTION

In their fundamental paper [1] Gurtin and MacCamy introduced a non-linear theory of population dynamics with age dependence, and in Ref. [2] discussed some applications. It was conjectured that under certain circumstances no Hopf bifurcation into stable orbits would be possible. A special case of this problem was considered in Refs [3, 4], but our purpose is to consider the general case and to extend previously obtained results. During the course of this analysis a necessary condition for Hopf bifurcation arises naturally, and an algorithm is produced in the appendix which enables us to determine this necessary condition for arbitrary systems of differential equations.

The theory is based on the equations [2, 5]

$$\frac{\partial u}{\partial t}+\frac{\partial u}{\partial a}-\bar{\mu}u=0 \tag{1}$$

$$B(t)=u(o,t)=\int_0^\infty \bar{\beta}\,[a,P(t)]\,u(a,t)\,\mathrm{d}a$$

$$P(t)=\int_0^\infty u(a,t)\mathrm{d}a$$

$$u(a,o)=u_0(a),$$

where $u(a, t)$ is the age distribution of some population, i.e. the distribution of individuals of age a at time t, $P(t)$ the total population, $B(t)$ the birth rate, $\bar{\beta}(a, P)$ the fertility function, $\bar{\mu}(a, P)$ the mortality function and $u_0(a)$ the initial age distribution.

Following Ref. [2], we shall consider the special case where the fertility function is given by

$$\bar{\beta}=\beta(P,\sigma)f(a)\exp(-\alpha a),$$

where β is a positive class C^1 function with a non-positive derivative with respect to P, denoted by $\dot{\beta}$, σ is a parameter (or set of parameters), $f(a)$ is a polynomial of degree n, and α a positive parameter.

Furthermore, we shall assume that the mortality function is age-independent, i.e. that

$$\bar{\mu}(a,P)=\mu(P,\sigma),$$

where μ is a positive class C^1 function, usually concave upwards in P.

As is well-known, the problem (1) could be explicitly solved if $B(t)$ were known, which it is not. So, following Ref. [2], a technique of weighting functions may be used to reduce problem (1) to an equivalent problem involving ordinary differential equations from which, theoretically at least, $B(t)$ may be obtained. At the very least we may obtain information concerning the behaviour of

P. We shall determine conditions under which Hopf bifurcation could take place for suitable values of σ.

We introduce the functions

$$K^i(t) = \int_0^\infty u(a,t) f^{(i)}(a) e^{-\alpha a}\, da,$$

where $f^{(i)}(a)$ denotes the ith derivative of $f(a)$, for $0 \leqslant i \leqslant n$. [Note that $B(t) = \beta(P,\sigma)K^0$.] On integrating equation (1), and equation (1) multiplied by $e^{-\alpha a} f^{(i)}(a)$, with respect to a, we obtain respectively

$$\begin{aligned} P' &= -\mu(P,\sigma)P + \beta(P,\sigma)K^0, \qquad (2)\\ K'^i &= \beta(P,\sigma) f^{(i)}(o)K^0 - [\alpha + \mu(P,\sigma)]K^i + K^{i+1}, \quad 0 \leqslant i \leqslant n-1,\\ K'^n &= \beta(P,\sigma) f^{(n)}(o)K^0 - [\alpha + \mu(P,\sigma)]K^n. \end{aligned}$$

We now specialize to the biologically realistic situation where $f(o) = 0$ (the less realistic case is dealt with in Refs [3, 4]), and with no loss of generality we assume $f^{(n)}(o) = 1$ (by multiplying β with a suitable factor), which makes K^n simply the Laplace transform of u with respect to a. At an equilibrium point (P_0, K_0^i) the r.h.s. of equation (2) is zero, so that

$$K_0^n = \beta(P_0,\sigma) f^{(n)}(o) K_0^0 [\alpha + \mu(P_0,\sigma)]^{-1}, \qquad (3)$$

$$K_0^{i+1} = -\beta(P_0,\sigma) f^{(i)}(o)K_0^0 + [\alpha + \mu(P_0,\sigma)]K_0^i, \quad 0 \leqslant i \leqslant n-2, \qquad (4)$$

$$K_0^0 = \mu(P_0,\sigma)P_0[\beta(P_0,\sigma)]^{-1}. \qquad (5)$$

It then follows easily from equation (3) that

$$\begin{aligned} K_0^n = -\beta(P_0,\sigma)K_0^0\{f^{n-1}(o) + [\mu(P_0,\sigma)+\alpha] f^{n-2}(o) + \cdots \\ \cdots + [\mu(P_0,\sigma)+\alpha]^{(n-1)} f^{(1)}(o) + [\mu(P_0,\sigma)+\alpha]^n K_0^0\}, \end{aligned}$$

and so from equation (2) we have

$$\begin{aligned} \beta(P_0,\sigma)\{f^{(n)}(o) + f^{n-1}(o)[\mu(P_0,\sigma)+\alpha] + \cdots \\ \cdots + f^{(1)}(o)[\mu(P_0,\sigma)+\alpha]^{n-1}\} - [\mu(P_0,\sigma)+\alpha]^{n+1} = 0. \qquad (6) \end{aligned}$$

That this equation has a solution $P_0 > 0$ is a necessary and sufficient condition for the system (2) to have a suitable equilibrium point, since equations (3)–(5) will then determine K_0^i. By the implicit function theorem a necessary and sufficient condition ensuring that such a solution P_0 exists is that the derivative of the l.h.s. of equation (6) be non-zero at P_0, and as we shall see, it turns out that for bifurcation to take place it is necessary that this derivative be negative at P_0.

We now introduce the variables $x = P - P_0$, $y_i = K^i - K_0^i$, so that system (2) becomes

$$\begin{aligned} x' &= -\mu(x+P_0,\sigma)[x+P_0] + \beta(x+P_0,\sigma)[y+K_0^0]\\ y_i' &= \beta(x+P_0,\sigma) f^i(o)[y_0+K_0^0] - [\alpha + \mu(x+P_0,\sigma)][y_i + K_o^i] + y_{i+1} + K_0^{i+1}\\ y_n' &= \beta(x+P_0,\sigma) f^{(n)}(o)[y_0+K_0^0] - [\alpha+\mu(x+P_0,\sigma)][y_n + K_0^n]. \qquad (7) \end{aligned}$$

The system linearized around the origin is easily shown to be

$$\begin{aligned} x' &= [-\mu(P_0,\sigma) - \dot\mu(P_0,\sigma)P_0 + \dot\beta(P_0,\sigma)\mu(P_0,\sigma)\beta^{-1}(P_0,\sigma)P_0]x + \beta(P_0,\sigma)y_0\\ y_i' &= [f^i(o)\dot\beta(P_0,\sigma)K_0^0 - \dot\mu(P_0,\sigma)K_0^i]x + f^{(i)}(o)\beta(P_o,\sigma)y_0\\ &\quad - [\alpha + \mu(P_0,\sigma)]y_i + y_{i+1}, \quad 0 \leqslant i \leqslant n-1,\\ y_n' &= [f^{(n)}(o)K_0^0\dot\beta(P_0,\sigma) - K_0^n\dot\mu(P_0,\sigma)]x + \beta(P_0,\sigma)f^n(o)y_0 - [\alpha+\mu(P_0,\sigma)]y_n, \qquad (8) \end{aligned}$$

where "$\cdot$" denotes differentiation with respect to P.

For convenience we shall write f^i for $f^{(i)}(o)$ and μ, β for $\mu(P_0,\sigma)$, $\beta(P_0,\sigma)$ and similarly for their derivatives, bearing in mind that we have suppressed the parameter σ. We also write $\wedge$ for $\mu + \alpha$ and A for $\dot\mu - \mu\beta^{-1}\dot\beta$.

Evaluating the characteristic equation of equation (8) is tedious but not difficult. It turns out to be

$$[\lambda + \mu + (\dot{\mu} - \mu\beta^{-1}\dot{\beta})P_0][(\lambda + \wedge)^{n+1} - \beta\{f^1(\lambda + \wedge)^{n-1} + f^2(\lambda + \wedge)^{n-2} + \cdots$$
$$\cdots + f^n\}] + \beta[\dot{\mu}K_0^0\{(\lambda + \wedge)^n + (\lambda + \wedge)^{n-1}\wedge + (\lambda + \wedge)^{n-2}(\wedge^2 - \beta f^1) + \cdots$$
$$\cdots + (\lambda + \wedge)^{n-3}(\wedge^3 - \beta f^1 - \beta f^2) + \cdots + (\lambda + \wedge)(\wedge^{n-1} - \wedge^{n-3}\beta f^1 - \cdots$$
$$\cdots - \wedge\beta f^{n-3} - \beta f^{n-2}) + (\wedge^n - \wedge^{n-2}\beta f^1 - \wedge^{n-3}\beta f^2 - \cdots - \wedge\beta f^{n-2} - \beta f^{n-1})\} - \cdots$$
$$\cdots - \dot{\beta}K_0^0\{f^n + f^{n-1}(\lambda + \wedge) + \cdots + f^2(\lambda + \wedge)^{n-2} + f^1(\lambda + \wedge)^{n-1}\}] = 0. \tag{9}$$

Making use of equation (6) we can show that the constant term in this polynomial in λ is given by

$$K_0^0[\beta\dot{\mu}\{(n+1)\wedge^n - \beta[(n-1)\wedge^{n-2}f^1 + (n-2)\wedge^{n-3}f^2 + \cdots$$
$$\cdots + 2\wedge f^{n-2} + f^{n-1}]\} - \dot{\beta}\wedge^{n+1}]. \tag{10}$$

For Hopf bifurcation to take place for some value σ_0 of the parameter σ, the following conditions are necessary and sufficient:

The characteristic roots of equation (9) must consist of n real, negative roots and one conjugate complex pair $\lambda_1 \pm i\lambda_2$, with $\lambda_1 \leqslant 0$ and $\lambda_2 > 0$. These roots of equation (9) obviously depend on σ, and if for some value σ_0 the complex roots become purely imaginary, and at the same time $\partial\lambda_1(\sigma_0)/\partial\sigma > 0$, then Hopf bifurcation will take place [6, p. 131].

For $\sigma = \sigma_0$ the characteristic polynomial must obviously have only positive coefficients. We have thus obtained the first necessary conditions for bifurcation to be possible. We shall refer again especially to the constant term, which from equation (10) implies that at σ_0

$$\beta\dot{\mu}[(n+1)\wedge^n - \beta\{(n-1)\wedge^{n-2}f^1 + (n-2)\wedge^{n-3}f^2 + \cdots$$
$$\cdots + 2\wedge f^{n-2} + f^{n-1}\}] - \dot{\beta}\wedge^{n+1} > 0. \tag{11}$$

(As we remarked earlier, this implies that the derivative of the l.h.s. of equation (6) be negative.)

We note, again, that for Hopf bifurcation to take place it is necessary that the roots of the characteristic equation (9) be of a certain form, namely n real negative roots and one conjugate complex pair that becomes purely imaginary for some value σ_0. This is, of course, true for any problem of the above nature—Hopf bifurcation can only take place if the roots (of the characteristic equation of the linearized system of an arbitrary initial system of first order differential equations) are of the form described above. It is very easily seen that $\lambda^2 + a\lambda + b = 0$ will have such roots iff $a = 0$, $b > 0$ for $\sigma = \sigma_0$, while $\lambda^3 + \alpha\lambda^2 + b\lambda + c = 0$ will have such roots only if $a, b, c > 0$, $ab - c = 0$ for σ_0, and $\lambda^4 + a\lambda^3 + b\lambda^2 + c\lambda + d = 0$ will have such roots only if $a, b, c, d > 0$ and $c(ab - c) - a^2d = 0$ and so on. The question arises in general: what conditions are necessary to ensure that an arbitrary polynomial will have roots of the kind described above? These conditions are vital in *any* problem involving Hopf bifurcation, since they obviously serve to determine the value σ_0 of the bifurcation parameter. We have produced an algorithm in the Appendix which enables us to construct these conditions for all values of n. The algorithm is clumsy, and could clearly be improved upon, but is extremely useful in the absence of anything better.

Returning to the problem under consideration, we apply those necessary conditions to a special case, since the general case involves an inordinate amount of calculation.

As a first illustration, let us choose the simplest case, where $n = 1$, i.e. $f(a) = a$. For this value the "equilibrium point" equation (6) becomes

$$\beta(P_0, \sigma) - [\mu(P_0, \sigma) + \alpha]^2 = 0, \tag{12}$$

while the characteristic equation is given by

$$\lambda^3 + \{2\wedge + \mu + AP_0\}\lambda^2 + \{2\mu\wedge + 2\wedge AP_0 + \mu\dot{\mu}P_0\}\lambda + \dot{\mu}P_0[2\wedge\dot{\mu} - \dot{\beta}] = 0. \tag{13}$$

For this equation to have suitable roots, i.e. one real negative root and one pair of complex roots which become imaginary at σ_0, it is necessary (see the Appendix) that

$$2 \wedge \dot{\mu} - \dot{\beta} > 0, \tag{14}$$

at σ_0 and that

$$[2 \wedge + \mu + AP_0]\,[2\mu \wedge + 2 \wedge AP_0 + \mu\dot{\mu}P_0] - \mu P_0\,[2 \wedge \dot{\mu} - \dot{\beta}] = 0,$$

for some value σ_0.

We can rewrite this equation as

$$A[2 \wedge A + \mu\dot{\mu}]P_0^2 + [\dot{\mu}(3\mu + 2\alpha)^2 - \mu\dot{\beta}(7\mu + 3\alpha) \wedge^{-1}]P_0 + 2(2 \wedge + \mu) \wedge \mu = 0, \tag{15}$$

and it becomes immediately obvious that if $\dot{\mu}(P_0, \sigma) \geqslant 0$ for all σ, all coefficients of powers of P_0 are positive, and therefore for no value of σ can this equation be satisfied. Hence if such a σ_0 exists, it follows that

$$\dot{\mu}(P_0, \sigma_0) < 0.$$

Furthermore, if from condition (14) we set

$$W \equiv 2\,\dot{\mu} - \dot{\beta} > 0,$$

where W is introduced purely for convenience, we may rewrite equation (15) as

$$\begin{aligned}[]
[\dot{\mu} \wedge (\alpha - \mu) + \mu W]\,[\dot{\mu} \wedge^2 (2\alpha - \mu) + 2 \wedge \mu W]\,P_0^2 + [\dot{\mu}(4\alpha^2 + 6\mu\alpha - 5\mu^2) \\
+ \mu(3 \wedge + 4\mu) \wedge^{-1} W]\,\beta^2 P_0 + 2(2 \wedge + \mu) \wedge \mu\beta^2 = 0,
\end{aligned} \tag{15$'$}$$

and it is readily seen that if $\mu \geqslant 2\alpha$ the coefficients of all powers of P are positive, and hence equation (15) can not be satisfied for any σ. Hence a necessary condition for the solution of equation (15) to exist, and thus Hopf bifurcation to be possible, is that

$$\mu(P_0, \sigma_0) < 2\alpha.$$

A far more useful special case occurs when $n = 2$, i.e. when

$$f(a) = ra + sa^2,$$

where $s > 0$, since we have more parameters with which to model the fertility function $\bar{\beta}(a, P)$.

If the fertility function which we wish to model increases from 0 to a maximum value M at $a = c$, and then decreases towards 0, it is readily seen that such a function can be approximated by

$$y = 2M\mathrm{e}^{c\alpha}(\alpha c - 1)c^{-2}\left[\frac{c}{2}(2 - \alpha c)\,(\alpha c - 1)^{-1}\,a + \frac{1}{2}a^2\right]\mathrm{e}^{-\alpha a},$$

which, provided $1 < \alpha c \leqslant 2$, will also increase from 0 to a maximum M at $a = c$, and then decay toward 0. By suitably multiplying $\beta(P, \sigma)$ by $2\,\mathrm{M}\ \mathrm{e}^{c\alpha}(\alpha c - 1)c^{-2}$ we can therefore assume that $f(a) = ka + \frac{1}{2}a^2$, where $k = \frac{1}{2}c(2 - \alpha c)\,(\alpha c - 1)^{-1}$. (We are still free to choose α to model the decay towards 0 as well as we can within the constraints $1 < \alpha c \leqslant 2$.)

For this value of f, the "equilibrium point" condition (6) becomes

$$\beta[1 + k \wedge] - \wedge^3 = 0, \tag{16}$$

while the characteristic equation is given by

$$\begin{aligned}[]
[\lambda + \mu + AP_0]\,[(\lambda + \wedge)^3 - \beta\{k(\lambda + \wedge)\} + 1] + \beta K_0^0\,[\dot{\mu}\{(\lambda + \wedge)^2 + (\lambda + \wedge) \wedge \\
+ \wedge^2 - \beta k\} - \dot{\beta}\{1 + k(\lambda + \wedge)\}] = 0.
\end{aligned} \tag{17}$$

With the help of equations (16) and (5) this equation can be rewritten as

$$\begin{aligned}
\lambda^4 + \lambda^3\{3 \wedge + \mu + AP_0\} + \lambda^2\{3 \wedge^2 - \beta k + 3 \wedge \mu + 3 \wedge AP_0 + \mu P_0 \dot{\mu}\} \\
+ \lambda\{3 \wedge^2\mu - \beta k\mu + 3 \wedge^2 AP_0 - \beta kAP_0 + 3 \wedge \mu P_0 \dot{\mu} - \mu k\dot{\beta}P_0\} \\
+ \mu P_0\,[\dot{\mu}(3 \wedge^2 - \beta k) - \dot{\beta}(1 + k \wedge)] = 0.
\end{aligned} \tag{18}$$

Rewriting this polynomial in the obvious manner as $\lambda^4 + a\lambda^3 + b\lambda^2 + c\lambda + d$, a necessary condition for equation (18) to have two real negative roots and one pair of imaginary roots is given by (see Appendix)

$$c(ab - c) - a^2 d = 0 \tag{19}$$

for some value σ_0 of σ. Routine but laborious calculation shows that equation (19) then becomes

$$\begin{aligned} &AP_0^3[3\dot{\mu}^2\{3\mu\wedge^2 + 2\wedge^3 + \mu^2\wedge + \beta\} - \mu\dot{\mu}\dot{\beta}\beta^{-1}\{14\wedge^3 + 9\wedge^2\mu + 3\beta + k\mu\beta\} \\ &\quad + \dot{\beta}^2\beta^{-2}8\wedge^3\mu^2] + P_0^2[\dot{\mu}^2(18\wedge^4 + 33\wedge^3\mu + 18\mu^2\wedge^2 + 3\mu^3\wedge + 9\wedge\beta + 3\mu\beta) \\ &\quad - \mu\dot{\mu}\dot{\beta}\beta^{-1}(36\wedge^4 + 51\wedge^3\mu + 18\mu^2\wedge^2 + 12\wedge\beta + 10\mu\beta) + \dot{\beta}^2\mu^2\beta^{-2}(18\wedge^4 + 18\wedge^3\mu \\ &\quad + 7\mu\beta + 3\wedge\beta) - k\dot{\beta}(k\mu\dot{\mu}\beta + \mu^2(\wedge + \mu)\dot{\mu} - 4\wedge\mu^3\beta^{-1}\dot{\beta})] \\ &\quad + P_0[\dot{\mu}\{12\wedge^5 + 36\wedge^4\mu + 33\wedge^3\mu^2 + 9\wedge^2\mu^3 + 12\wedge^2\beta + 18\wedge\mu\beta + 3\mu^2\beta + 3\beta^2\wedge^{-1}\} \\ &\quad - \mu\dot{\beta}\beta^{-1}\{9\wedge^5 + 37\wedge^4\mu + 20\wedge^3\mu^2 + 6\wedge^2\beta + 6\mu^2\beta + 10\mu\wedge\beta + 3\beta^2\wedge^{-1} + \mu\beta^2\wedge^{-2}\}] \\ &\quad + [6\wedge^3 + 9\wedge^2\mu + 3\wedge\mu^2 + 3\beta][2\wedge^2\mu + \mu\beta\wedge^{-1}] = 0. \end{aligned} \tag{20}$$

It is immediately obvious that if $\dot{\mu} \geqslant 0$ all coefficients of the various powers of P_0 are positive, and for no value of σ can equation (20) be satisfied. A necessary condition for bifurcation to take place is therefore that $\dot{\mu}(P_0, \sigma)$ takes on negative values, and that therefore $\dot{\mu}(P_0, \sigma_0) < 0$.

A further restriction on μ can be obtained as follows: from condition (11) we may write

$$W \equiv (3\wedge^2 - \beta k)\beta\dot{\mu}\wedge^{-3} - \dot{\beta} > 0,$$

where W is introduced purely for computational convenience. Equation (20) can be rewritten as

$$\begin{aligned} &P_0^3\wedge^{-4}\dot{\mu}[\wedge^3(\alpha - \mu) - \mu\beta][\dot{\mu}^2\{\wedge(6\alpha^2 - 7\alpha\mu + 2\mu^2) + \beta\wedge^{-2}(3\alpha^2 - 14\mu\alpha + 7\mu^2) \\ &\quad + \mu\beta^2\wedge^{-5}(6\mu - 3\alpha)\} + \dot{\mu}\mu\beta^{-1}W\{\wedge^2(14\alpha - 8\mu) + \beta\wedge^{-1}(3\alpha - 14\mu)\} \\ &\quad + 8W^2\wedge^3\mu^2\beta^{-2}] \\ &\quad + P_0^2[\{\wedge(16\mu^3 - 46\alpha\mu^2 + 11\mu\alpha^2 + 18\alpha^3) + \beta\wedge^{-2}(76\mu^3 - 43\mu^2\alpha - 25\mu\alpha^2 + 9\alpha^3) \\ &\quad + \mu\beta^2\wedge^{-5}(18\mu^2 + 13\mu\alpha - 16\alpha^2) + \beta^2\mu\wedge^{-8}(7\mu^2 + 5\mu\alpha + \alpha^2)\}\mu^2 - W\dot{\mu}\mu\beta^{-1}\{\wedge^2(52\mu^2 \\ &\quad - 54\mu\alpha - 37\alpha^2) + \beta\wedge^{-1}(56\mu^2 + 19\mu\alpha - 10\alpha^2) + 6\mu\beta^2\wedge^{-4}(2\mu + \alpha)\} \\ &\quad + W^2\mu^2\beta^{-2}\{18\wedge^4 + 22\wedge^3\mu + 3\mu\beta + 3\wedge\beta\}] \\ &\quad + P_0[\dot{\mu}\{\wedge^2(12\alpha^3 + 54\alpha^2\mu + 31\alpha\mu^2 - 42\mu^3) + \beta\wedge^{-1}(12\alpha^3 + 27\alpha^2\mu - 36\alpha\mu^2 \\ &\quad - 83\mu^3) + \beta^2\wedge^{-4}(3\alpha^3 - 3\mu\alpha^2 - 27\mu^2\alpha - 27\mu^3)\} + \mu W\beta^{-1}\{9\wedge^5 + 37\wedge^4\mu \\ &\quad + 20\wedge^3\mu^2 + 6\wedge^2\beta + 6\mu^2\beta + 10\mu\wedge\beta + 3\beta^2\wedge^{-1} + \mu\beta^2\wedge^{-2}\}] \\ &\quad + [6\wedge^3 + 9\wedge^2\mu + 3\wedge\mu^2 + 3\beta][2\wedge^2\mu + \mu\beta\wedge^{-1}] = 0. \end{aligned} \tag{21}$$

It is readily seen that, if $\dot{\mu} < 0$, the coefficients of the different powers of P_0 are all positive for $\mu \geqslant 2\alpha$, and no solution of equation (21) is possible. Hence we have obtained the further condition that $\mu(P_0, \sigma_0) < 2\alpha$, which of course excludes Hopf bifurcation in those cases where $\mu(P, \sigma) \geqslant 2\alpha$.

RESULTS

We have now established the following results:

For both the case $n = 1$ and $n = 2$ Hopf bifurcation can only take place if the function $\mu(P, \sigma)$ has a (locally) negative derivative, if condition (10) is satisfied and if it dips down to below the value 2α. The first condition does not always occur in nature as in most cases mortality increases with population. However, we consider the case of a well-mixed reaction vessel in which a biological population is living. A reagent stream free of this organism flows into the tank and a product stream flows out, containing both living and dead organisms. The mortality function must then be defined in such a way that it accounts for both natural mortality and elimination by being carried out in the effluent stream. This means that $\mu(P, \sigma)$ should be quite large for small P, decrease as P increases, and increase as P increases to non-optimal levels.

Such a function could well be of the form $ae^P - c + be^{-P}$, where a, b, c are positive functions of σ and $4ab > c^2$ to ensure that μ stays positive.

On the other hand, the fertility function $\beta(P, \sigma)$ could well be a steadily decreasing function of P, something like Be^{-kP}. (A considerably simpler and perhaps less realistic model is discussed in Ref. [3].)

Such a model can indeed lead to Hopf bifurcation, which we illustrate as follows:

$$\text{let } n = 1, \quad \text{so that } f(a) = a, \quad \text{and let } \mu = (c - \alpha)e^{-\sigma}e^{P} - c + (3\alpha - c)e^{\sigma}e^{-P},$$

while $\beta = (3\alpha - c)^2 e^{2\sigma} e^{-2P}$.

This is obviously very synthetic, but biologically not completely impossible. We assume $c, \sigma > 0$ and, to ensure $\mu > 0$, we assume $\frac{6}{5}\alpha < c < 2\alpha$, where α is of course the original parameter introduced in β.

On substituting into equation (5) and (6) we find

$$P_0 = \sigma, \quad K_0^0 = (2\alpha - c)(3\alpha - c)^{-1}, \quad K_0^1 = (3\alpha - c)^{-1}(2\alpha - c)\sigma.$$

It is now a simple matter to show that the corresponding linearized system (8) has the characteristic polynomial

$$\lambda^3 + (8\alpha - 3c)^2 \lambda + [2(2\alpha - c)(3\alpha - c) - 2(2\alpha - c)^2\sigma] + 2(2\alpha - c)(3\alpha - c)(c - \alpha)\sigma = 0.$$

The necessary and sufficient condition that the characteristic roots are of the required form is given by equation (15) as

$$(8\alpha - 3c)[2(2\alpha - c)(3\alpha - c) - 2(2\alpha - c)^2\sigma] - 2(2\alpha - c)(3\alpha - c)(c - \alpha)\sigma = 0,$$

which is satisfied by the value of σ given by

$$\sigma_0 = (8\alpha - 3c)(3\alpha - c)(13\alpha^2 - 10\alpha c + 2c^2)^{-1}.$$

For this value of σ the characteristic roots are given by

$$\lambda_1 = -(8\alpha - 3c) \quad \text{and} \quad \lambda_2 = \pm i[2(2\alpha - c)(3\alpha - c)^2(c - \alpha)(13\alpha^2 - 10\alpha c + 2c^2)^{-1}]^{1/2}.$$

It is not difficult also to show that

$$\left.\frac{\partial \lambda_1(\sigma)}{\partial \sigma}\right|_{\sigma_0} = 2(2\alpha - c)(13\alpha^2 - 10\alpha c + 2c^2)^{-1} > 0,$$

so that all conditions for Hopf bifurcation are met and bifurcation will indeed take place at σ_0. Whether this bifurcation can lead to stable limit cycles is a different matter, but initial computer simulations show that in the above example stable limit cycles do appear to arise provided we take c close enough to 2α.

REFERENCES

1. M. E. Gurtin and R. C. MacCamy, Non-linear age dependent population dynamics. *Archs rational Mech. Analysis* **54**, 281–300 (1974).
2. M. E. Gurtin and R. C. MacCamy, Some simple models for nonlinear age-dependent population dynamics. *Math. Biosci.* **43**, 199–211 (1979).
3. J. C. Frauenthal, and K. E. Swick, Stability of biochemical reaction tanks. *Comput. Math. Applic.* **9**(3), 499–506 (1983).
4. J. H. Swart, On the stability of a nonlinear, age-dependent population model, as applied to a biochemical reaction tank. *Math. Biosci.* **80**(1), 47–56 (1986).
5. F. Hoppensteadt, Mathematical theories of population: demographics, genetics and epidemics. *Soc. Ind. Appl. Math.* Philadelphia (1975).
6. J. E. Marsden and M. McCracken, The Hopf bifurcation and its applications. *Appl. Maths Series*, Vol. 19, Springer, New York (1970).

APPENDIX

An Algorithm for Establishing Necessary Conditions for Hopf Bifurcation to Take Place

In considering a system of the form

$$\dot{x}_i = F(x_j, \sigma), \quad i = 1, \ldots, (n+2),$$

with an equilibrium point at the origin, the linearized form of this system is given by

$$\dot{x}_i = A_{ij}(\sigma) x_j,$$

with a corresponding characteristic polynomial of degree $n+2$. In order that Hopf bifurcation may take place it is necessary that the roots of this polynomial consist of n negative real values and one conjugate complex pair with real part negative, and which is such that for some value σ_0 the complex pair becomes purely imaginary. This then leads to a condition [involving $A_{ij}(\sigma)$] which has to be satisfied by σ for some value σ_0, and it is of some interest to establish such a condition for arbitrary systems.

Lemma

For the polynomial $Q = x^{n+2} + A_1 x^{n+1} + A_2 x^n + \cdots + A_{n+1} x + A_{n+2}$ to have two imaginary roots and n negative real roots it is necessary that the coefficients A_i be non-negative and satisfy the condition that is obtained by eliminating α^2 from the relevant pair of equations given below.

If $n = 2m$,

$$A_{2m+2} - \alpha^2 A_{2m} + \alpha^4 A_{2m-2} \cdots (-1)^m \alpha^{2m} A_2 - (-1)^m \alpha^{2m+2} = 0$$
$$A_{2m+1} - \alpha^2 A_{2m-1} + \alpha^4 A_{2m-3} - \cdots (-1)^m \alpha^{2m-2} A_3 + (-1)^m \alpha^{2m} A_1 = 0. \tag{A.1a}$$

If $n = 2m+1$,

$$A_{2m+2} - \alpha^2 A_{2m} + \alpha^4 A_{2m-2} - \cdots + (-1)^m \alpha^{2m} A_2 - (-1)^m \alpha^{2m+2} = 0.$$
$$A_{2m+3} - \alpha^2 A_{2m+1} + \alpha^4 A_{2m-1} - \cdots + (-1)^m \alpha^{2m} A_3 - (-1)^m \alpha^{2m+2} A_1 = 0. \tag{A.1b}$$

The result follows trivially from the remainder theorem. However, for later reference we introduce some notation: Let $\pm i\alpha$ be the imaginary roots of Q and let $-a_i$ be the negative real roots of Q, and let

$$p_1 = \sum_1^n a_i, \; p_2 = \sum_{i_1 \neq i_2}^n a_{i_1} a_{i_2},$$
$$p_3 = \sum_{i_1 \neq i_2 \neq i_3}^n a_{i_1} a_{i_2} a_{i_3}, \ldots p_n = \sum_{i_1 \neq i_2 \neq \ldots i_n}^n a_{i_1} a_{i_2} \ldots a_{i_n} = a_1 a_2 \ldots a_n. \tag{A.2}$$

It is then easily seen that

$$Q = x^{n+2} + p_1 x^{n+1} + (p_2 + \alpha^2) x^n + (p_3 + \alpha^2 p_1) x^{n-1} + \cdots + (p_n + \alpha^2 p_{n-2}) x^2 + \alpha^2 p_{n-1} x + \alpha^2 p_n. \tag{A.3}$$

It then follows readily that

$$A_1 = p_1, \quad A_2 = p_2 + \alpha^2, \quad A_3 = p_3 + \alpha^2 p_1, \quad A_4 = p_4 + \alpha^2 p_2, \ldots$$
$$A_n = p_n + \alpha^2 p_{n-2}, \quad A_{n+1} = \alpha^2 p_{n-1}, \quad A_{n+2} = \alpha^2 p_n. \tag{A.4}$$

(By eliminating p_i from this system we would obtain equations (A.1). We note that from equation (A.3) it follows directly that all $A_i > 0$ is a necessary condition.

It is clear that by suitably reducing the two equations in equation (A.1a) or (A.1b) we can indeed eliminate α^2 and obtain a necesary condition on the A_i in order that α^2 exist (and hence that the roots of Q are as desired). This is extremely laborious for n larger than 4 or 5, and our aim is to find an algorithm whereby it can be done mechanically and with less labour.

First we illustrate the above result with some special cases.

For $n = 1$:

$$Q = x^3 + A_1 x^2 + A_2 x + A_3.$$

From equations (A.1b) it follows that A_i must satisfy

$$A_2 - \alpha^2 = 0 \quad \text{and} \quad A_3 - \alpha^2 A_1 = 0$$

Eliminating α^2 leads to the condition

$$F_1 \equiv A_1 A_2 - A_3 = 0, \tag{A.5}$$

as being necessary for Q to have one pair of imaginary roots and one negative real root.

In the same way, if $n = 2$, $Q = x^4 + A_1 x^3 + A_2 x^2 + A_3 x + A_4$, it follows from equation (A.1) that the coefficients must satisfy

$$A_4 - \alpha^2 A_2 + \alpha^4 = 0 \quad \text{and} \quad A_3 - \alpha^2 A_1 = 0.$$

Eliminating α^2 leads to the necessary condition

$$F_2 \equiv A_3 (A_1 A_2 - A_3) - A_1^2 A_4 = 0. \tag{A.6}$$

Similarly if $n = 3$, the conditions become

$$A_4 - \alpha^2 A_2 + \alpha^4 = 0 \quad \text{and} \quad A_5 - \alpha^2 A_3 - \alpha^4 A_1 = 0,$$

with necessary condition

$$F_3 \equiv A_4 [A_3 (A_1 A_2 - A_3) - A_1^2 A_4] - A_5 [A_5 + A_2 (A_1 A_2 - A_3) - 2A_1 A_4]. \tag{A.7}$$

It is of interest to develop an algorithm to construct this condition for further values of n, as the labour involved becomes somewhat tedious.

We note that the equations leading to equation (A.6) had one equation the same as those leading to equation (A.5), and similarly those leading to equation (A.7) had one identical to those leading to equation (A.6). In general, let us assume that we have found F_n, where $n = 2m + 1$, and we wish to establish F_{n+1}.

The equations leading to F_n are given by equation (A.1) as

$$A_{2m+2} - \alpha^2 A_{2m} + \cdots + (-1)^m \alpha^{2m} A_2 - (-1)^m \alpha^{2m+2} = 0, \tag{A.8}$$

$$A_{2m+3} - \alpha^2 A_{2m+1} + \cdots + (-1)^m \alpha^{2m} A_3 - (-1)^m \alpha^{2m+2} A_1 = 0, \tag{A.9}$$

while, again from equation (A.7), the equations leading to F_{n+1} would be

$$A_{2m+4} - \beta^2 A_{2m+2} + \cdots + (-1)^{m+1} A_2 \beta^{2m+2} - (-1)^{m+1} \beta^{2m+4} = 0, \tag{A.10}$$

$$A_{2m+3} - \beta^2 A_{2m+1} + \cdots - (-1)^{m+1} A_3 \beta^{2m} + (-1)^{m+1} \beta^{2m+2} A_1 = 0. \tag{A.11}$$

We note that equations (A.9) and (A.11) are identical, involving only the odd numbered coefficients A_i. On suitably subtracting equations (A.11) from (A.10) we obtain the equivalent equation

$$A_{2m+4} A_1 - \beta^2 (A_1 A_{2m+2} - A_{2m+3}) + \cdots - (-1)^{m+1} (A_1 A_2 - A_3) \beta^{2m+2} = 0. \tag{A.10$'$}$$

We note that equation (A.10′) is equivalent to equation (A.8) if in equation (A.8) we replace

$$\begin{aligned} &A_{2m+2} \text{ by } A_1 A_{2m+4} (A_1 A_2 - A_3)^{-1}, \\ &A_{2m} \text{ by } (A_1 A_{2m+2} - A_{2m+3})(A_1 A_2 - A_3)^{-1}, \\ &\quad\cdots \\ &A_2 \text{ by } (A_1 A_4 - A_5)(A_1 A_2 - A_3)^{-1} \end{aligned} \tag{A.12}$$

and by eliminating α^2 from the resulting equation and equation (A.9) we will obtain the same necessary condition as we would by eliminating β^2 from equations (A.10′) and (A.11). Hence by substituting as in equation (A.12) into F_n, we will obtain F_{n+1}. As an illustration, consider $n = 3$, with F_3 given in equation (A.7). We then substitute in equation (A.7) as in equation (A.12).

$$\begin{aligned} &A_4 \text{ by } A_1 A_6 (A_1 A_2 - A_3)^{-1}, \\ &A_2 \text{ by } (A_1 A_4 - A_5)(A_1 A_2 - A_3)^{-1}, \end{aligned}$$

upon which F_3 becomes

$$\begin{aligned} &A_1 A_6 (A_1 A_2 - A_3)^{-1} [A_3 \{A_1 (A_1 A_4 - A_5)(A_1 A_2 - A_3)^{-1} - A_3\} - A_1^2 A_1 A_6 (A_1 A_2 - A_3)^{-1}] \\ &\quad - A_5 [A_5 + (A_1 A_4 - A_5)(A_1 A_2 - A_3)^{-1} \{A_1 (A_1 A_4 - A_5)(A_1 A_2 - A_3)^{-1} - A_3\} \\ &\quad - 2A_1 A_1 A_6 (A_1 A_2 - A_3)^{-1}] = 0, \end{aligned}$$

which reduces to

$$\begin{aligned} &A_5 [A_4 \{A_3 (A_1 A_2 - A_3) - A_1^2 A_4\} - A_5 \{A_5 + A_2 (A_1 A_2 - A_3) - 2A_1 A_4\}] \\ &\quad - A_6 [A_3 \{A_3 (A_1 A_2 - A_3) - A_1^2 A_4\} + A_1^3 A_6 - 2A_1 A_5 (A_1 A_2 - A_3) + A_1 A_3 A_5] = 0. \end{aligned}$$

By exactly similar arguments we may find the algorithm whereby we can determine F_{n+1} from F_n if $n = 2m$. It is easily shown that we must replace as follows:

$$\begin{aligned} &A_{2m+1} \text{ by } A_1 A_{2m+2} - A_{2m+3} \\ &A_{2m-1} \text{ by } A_1 A_{2m} - A_{2m-1} \\ &\quad\cdots \\ &A_3 \text{ by } A_1 A_4 - A_5 \\ &A_1 \text{ by } A_1 A_2 - A_3, \end{aligned} \tag{A.13}$$

in other words, A_{2k+1} by $A_1 A_{2k+2} - A_{2k+3}$ for $k > 0, 1, \ldots, m$.

For example to find F_3 from F_2, replace A_1 by $A_1 A_2 - A_3$ and A_3 by $A_1 A_4 - A_5$ in equation (A.6), leading to

$$(A_1 A_4 - A_5)[(A_1 A_2 - A_3) A_2 - (A_1 A_4 - A_5)] - (A_1 A_2 - A_3)^2 A_4 = 0,$$

which obviously reduces to the F_3 given in equation (A.7).

A tantalizing pattern appears to be developing in these necessary conditions, especially if we write them as

$$\begin{aligned} &F_0 = A_1 \\ &F_1 = A_2 F_0 - A_3 \\ &F_2 = A_3 F_1 - A_4 A_1 F_0 \\ &F_3 = A_4 F_2 - A_5 [A_2 F_1 - 2A_4 F_0 + A_5] \\ &F_4 = A_5 F_3 - A_6 [A_3 F_2 - 2A_5 A_1 F_1 + A_3 A_5 F_0 + A_1^3 A_6] \\ &F_5 = A_6 F_4 - A_7 [A_4 F_3 - 2A_6 A_2 F_2 + A_4 A_6 A_1 F_1 + A_7^2 - A_6 (2A_1^2 A_6 \\ &\qquad + A_5 (2A_1 A_2 - 3F_1) + A_7 (A_2 (A_2 F_1 + A_5 - A_1 A_4) + 3A_1 A_6 - 2A_4 F_1))]. \end{aligned} \tag{A.14}$$

It would be interesting to determine the exact formula for F_{n+1} in terms of $F_0, \ldots, F_n$, but we have not yet been able to do so. However, by using the relevant algorithms given in equations (A.12) and (A.13) we can construct F_{n+1} from F_0, $F_1, \ldots, F_n$.

A different approach to the construction of F_{n+1} in terms of F_k could be the following.

From equation (A.2) it follows that

$$\begin{aligned} A_1 &= p_1, \\ A_2 &= p_2 + \alpha^2, \\ A_3 &= p_3 + \alpha^2 p_1, \\ A_k &= p_k + \alpha^2 p_{k-2}, \\ A_n &= p_n + \alpha^2 p_{n-2}, \end{aligned} \tag{A.15}$$

$$A_{n+1} = \alpha^2 p_{n-1}, \tag{A.16}$$

$$A_{n+2} = \alpha^2 p_n. \tag{A.17}$$

Disregarding (A.16) we have $n+1$ equations in the $n+1$ variables p_i, α^2, which can be solved for α^2 and p_i in terms of $A_1, A_2, \ldots A_n, A_{n+2}$. The omitted equation (A.16) then provides a "consistency condition"

$$A_{n+1} - \alpha^2(A_1, \ldots, A_n, A_{n+2}) p_{n-1}(A_1, \ldots, A_n, A_{n+2}) = 0, \tag{A.16$'$}$$

which we will designate as $H_n = 0$. (Obviously H_n will be equivalent to the F_n obtained earlier.) As an illustration, consider $n = 2$: equation (A.15) then becomes

$$A_1 = p_1, \quad A_2 = p_2 + \alpha^2, \quad A_3 = \alpha^2 p_1, \quad A_4 = \alpha^2 p_2.$$

It is easily found that $p_1 = A_1, p_2 = \frac{1}{2}(A_2 \pm \sqrt{A_2^2 - 4A_4})$, $\alpha^2 = \frac{1}{2}(A_2 \mp \sqrt{A_2^2 - 4A_4})$ and so from the omitted equation (A.16) we obtain the consistency condition

$$H_2 \equiv A_3 - \frac{1}{2}(A_2 \pm \sqrt{A_2^2 - 4A_4})\,(A_1),$$

which is equivalent to

$$F_2 \equiv A_3(A_1 A_2 - A_3) - A_1^2 A_4 = 0,$$

the condition obtained earlier.

The interesting aspect of this approach occurs naturally when we consider the situation which arises for H_{n+1}: the system (A.15) now becomes

$$A_1 = p_1, \quad A_2 = p_2 + \alpha^2, \quad A_3 = p_3 + \alpha^2 p_1, \quad \ldots, \quad A_n = p_n + \alpha^2 p_{n-2}, \tag{A.18}$$

$$A_{n+1} = p_{n+1} + \alpha^2 p_{n-1}. \tag{A.19}$$

$$A_{n+2} = \alpha^2 p_n \tag{A.20}$$

$$A_{n+3} = \alpha^2 p_{n+1} \tag{A.21}$$

The remarkable fact is that (A.18) and (A.20) are identical to equation (A.15) with (A.17), hence in solving for p_i, we obtain the *same* values in both sets of equations. Eliminating p_{n+1} from equations (A.19) and (A.21) then provides a further "consistency" condition

$$A_{n+3} - \alpha^2 A_{n+1} + \alpha^4 p_{n-1} = 0$$

which can be written as

$$A_{n+3} - \alpha^2 H_n = 0.$$

We are then justified in writing

$$H_{n+1} = A_{n+3} - \alpha^2 H_n = 0. \tag{A.22}$$

This provides us with an alternative algorithm for obtaining the necessary condition for bifurcation. We illustrate with $n = 2$, where we have already obtained $H_2 = A_3 - \frac{1}{2}A_1\,[A_2 \pm (A_2^2 - 4A_4)^{1/2}]$. Then from equation (A.22) it follows that

$$H_3 = A_5 - \alpha^2\{A_3 - \tfrac{1}{2}A_1\,[A_2 \pm (A_2^2 - 4A_4)^{1/2}]\}$$

and we know $\alpha^2 = A_2 \mp (A_2^2 - 4A_4)^{1/2}$. It is easily shown that $H_3 = 0$ is then equivalent to

$$F_2 \equiv A_4[A_3(A_1 A_2 - A_3) - A_1^2 A_4] - A_5[A_5 + A_2(A_1 A_2 - A_3) - 2A_1 A_4] = 0,$$

a result previously obtained.

In equation (A.22) we therefore have a powerful algorithm for obtaining H_{n+1} once H_n is known, with, of course, the distinct drawback that α^2 has to be calculated from equation (A.1), but this again *can* be done by suitable manipulation of the relevant two equations.

It is important to note that if $H_{n+1} = 0$, all the previous consistency expressions H_k, $k = 1, \ldots, n$, have to be positive (since $A_i > 0$). This provides us with a further set of necessary conditions on the A_i.

A further interesting aspect of the "consistency" conditions is the role they play in another necessary condition for Hopf bifurcation, namely that if the pair of complex roots of the relevant characteristic equation is given by $\lambda_1 \pm i\lambda_2$ then $\partial\lambda_1/\partial\sigma > 0$ at σ_0 [6, p. 131]. It transpires that the sign of $\partial\lambda_1/\partial\sigma$ at σ_0 is determined by $\partial F_n/\partial\sigma$ at σ_0, which is very useful since we can then obtain this value without finding λ_1 (which is of course wellnigh impossible in higher values of n).

Let the polynomial $P = x^{n+2} + A_1 x^{n+1} + A_2 x^n + \ldots + A_{n+1}x^1 + A_{n+2}$ have n negative real roots $-a_i$, and one pair of complex roots $\lambda = \lambda_1 + i\lambda_2$, $\bar{\lambda} = \lambda_1 - i\lambda_2$, where $\lambda_1 \leqslant 0$ and all these terms are functions of σ, and at σ_0 we have $\lambda_1 = 0$.

Then

$$P = (x - \lambda_1 - i\lambda_2)(x - \lambda_1 + i\lambda_2)(x + a_1)(x + a_2)\cdots(x + a_n),$$
$$= (x^2 - 2\lambda_1 x + |\lambda|^2)(x^n + p_1 x^{n-1} + p_2 x^{n-2} + \cdots + p_n)$$

where p_r is defined as before in equation (A.2).

Hence

$$\begin{aligned} P = {} & x^{n+2} + (p_1 2\lambda_1)x^{n+1} + x^n(p_2 2\lambda_1 p_1 + |\lambda|^2) \\ & + x^{n-1}(p_3 - 2\lambda_1 p_2 + |\lambda|^2 p_1) + \cdots \\ & \cdots + x^{n-k}(p_{k+2} - 2\lambda_1 p_{k+1} + |\lambda|^2 p_k) + \cdots \\ & \cdots + x(-2\lambda_1 p_n + |\lambda|^2 p_{n-1}) + |\lambda|^2 p_n. \end{aligned}$$

For P to have the required roots it is therefore necessary and sufficient that

$$\begin{aligned} A_1 &= p_1 - 2\lambda_1, \\ A_2 &= p_2 - 2\lambda_1 p_1 + |\lambda|^2, \\ A_k &= p_k - 2\lambda_1 p_{k-1} + |\lambda|^2 p_{k-2}, \\ &\cdots \\ A_n &= p_n - 2\lambda_1 p_{n-1} + |\lambda|^2 p_{n-2}, \\ A_{n+1} &= -2\lambda_1 p_n + |\lambda|^2 p_{n-1}, \\ A_{n+2} &= |\lambda|^2 p_n. \end{aligned}$$

On rewriting this set of $n+2$ equations as

$$\begin{aligned} A'_1 &\equiv A_1 + 2\lambda_1 = p_1, \\ A'_2 &\equiv A_2 + 2\lambda_1 p_1 = p_2 + |\lambda|^2, \\ A'_k &\equiv A_k + 2\lambda_1 p_{k-1} = p_k + |\lambda|^2 p_{k-2}, \\ A'_n &\equiv A_n + 2\lambda_1 p_{n-1} = p_n + |\lambda|^2 p_{n-2}, \\ A'_{n+1} &\equiv A_n + 2\lambda_1 p_n = |\lambda|^2 p_{n-1}, \\ A'_{n+2} &\equiv A_{n+2} = |\lambda|^2 p_n, \end{aligned} \tag{A.23}$$

we obtain a system which is identical in structure to equation (A.4), with $|\lambda|^2$ playing the role of α^2 and of course A'_k the role of A_k. From equation (A.4), a system of $n+2$ equations, we found it possible to eliminate the α^2, p_i to obtain a single condition

$$F_n(A_k) = 0.$$

It therefore follows immediately that an exactly similar relation will follow from equation (A.23), viz.

$$F_n(A'_k) = 0.$$

We have therefore obtained the relationship

$$F_n[A_1 + 2\lambda_1, A_2 + 2\lambda_1 p_1, \ldots, A_k + 2\lambda_1 p_{n-1}, \ldots, A_{n+1} + 2\lambda_1 p_n, A_{n+2}] = 0. \tag{A.24}$$

From the nature of equation (A.24) it is obvious that F will be analytic and hence we may expand it in a Taylor series in terms of λ_1. We denote the partial derivative of F_n with respect to the kth variable in its argument by $F_{n,k}$, and differentiation with respect to λ_1 by "′", so that equation (A.24) leads to

$$F_n(A_1, A_2 \ldots A_{n+2}) + [F_{n,1}2 + F_{n,2}(2\lambda_1 p_1)' + \cdots + F_{n,n+1}(2\lambda_1 p_n)' + F_{n,n+2}0]\lambda_1 + 0(\lambda_1^2) = 0.$$

On differentiating this equation with respect to σ, and evaluating the resulting expression at σ_0, where of course $\lambda_1 = 0$, we obtain

$$\frac{\partial F_n(A_k)}{\partial \sigma} + [F_{n,1}2 + 2F_{n,2}p_1 + \cdots 2F_{n,n+1}p_n]\frac{\partial \lambda_1}{\partial \sigma} = 0.$$

We have therefore established that at σ_0

$$\frac{\partial \lambda_1}{\partial \sigma} = \frac{-\partial F_n}{\partial \sigma}[2F_{n,1} + 2F_{n,2}p_1 + \cdots + 2F_{n,n+1}p_n]^{-1}, \tag{A.25}$$

so that once F_n has been obtained we have found $\partial\lambda_1/\partial\sigma$, without explicitly determining λ_1, and we may verify whether Hopf bifurcation will take place.